ELLISITES, AN UPPER ORDOVICIAN HELIOLITID CORAL INTERMEDIATE BETWEEN COCCOSERIDS AND PROPORIDS

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ABSTRACT. The Upper Ordovician heliolitid corals *Ellisites labechioides* gen. et sp. nov. and *E. astomata* (Flower) combine vesicular skeletal plates with zones of strongly dilated vertical trabeculae. In these characters they provide the first evidence of a phylogenetic link between the Coccoseridicae and Proporicae. They are referred to a new family, the Ellisitidae, and included in the Coccoseridicae, which necessitates taxonomic modification of the latter to include genera with vesicular skeletal plates. They show features most related to *Coccoseris* Eichwald, 1855, and to two of three species considered to have been erroneously referred to the stromatoporoid *Dermatostroma* Parks, 1910. Their substantially vesicular skeletal development can lead them to be mistaken for strongly cystose labechiid stromatoporoids.

RECENT publications (e.g. Bogoyavlenskaya and Boyko 1979, p. 31) have explored the relationships, real or apparent, between some heliolitid corals and some stromatoporoids. Nestor (1981) proposed that the close similarity between the dense trabecular skeleton of protaraeids (Heliolitoidea) and the fibro lamellar skeleton of lophiostromatids (Stromatoporoidea) was evidence of common origin. Similarly, he likened the cystose skeletons of proporids (Heliolitoidea) to those of labechiids (Stromatoporoidea). Stearn (1982) argued generally against these and other such morphological links. He suggested that the occurrence and stratigraphic distribution of stromatoporoids supported their evolution as a separate, unitary group, despite the '. . . plethora of linking forms . . .' (ibid., p. 515) illustrating morphological continuity between stromatoporoids and several other groups. The proposed relationship has also been rejected recently by Scrutton (1984, p. 114).

A new family of heliolitid corals that provides new information on one of these 'links' occurs in Upper Ordovician rocks on Anticosti Island, Quebec. It is significant for the resemblances it bears to several taxa of heliolitid corals and stromatoporoids. Its skeletal structures relate it unequivocally to the heliolitid *Coccoseris* Eichwald, 1855, and, in turn, to some species formerly referred to the stromatoporoid *Dermatostroma* Parks, 1910. Its morphological variability extends to forms appearing deceptively like primitive labechiid stromatoporoids. It also significantly occupies an intermediate position, not previously recorded (Nestor 1981, pp. 24–25), between heliolitids of substantially vesicular structure (Proporicae) and those strongly trabecular (Coccoseridicae or Protaraeida).

The few occurrences of fossils now considered to belong to this family are widely spread in North America, from Texas to eastern and northern Canada. Well-preserved material belonging to two species, one of them new, has been collected from Anticosti Island (text-fig. 1). In particular, specimens have been found in coral-rich limestones and shales near the top of the Vaureal Formation (Ashgill-Richmondian; Nowlan and Barnes 1981) of western and north-eastern Anticosti Island, in a bioherm in member 4 of the Ellis Bay Formation (Lake 1981; Ashgill-Gamachian; McCracken and Barnes 1981) of central Anticosti Island, and through the lower two-thirds of the Ellis Bay Formation, north-eastern Anticosti Island (text-fig. 2). The objectives of this paper, therefore, are to describe these taxa and to evaluate both their systematic relationships as a new group of heliolitid corals, and their deceptive mimicry of labechiid stromatoporoids.

Further information on the bio- and lithostratigraphic setting of these corals can be found in Bolton (1972, 1981) and Petryk (1979, 1981).
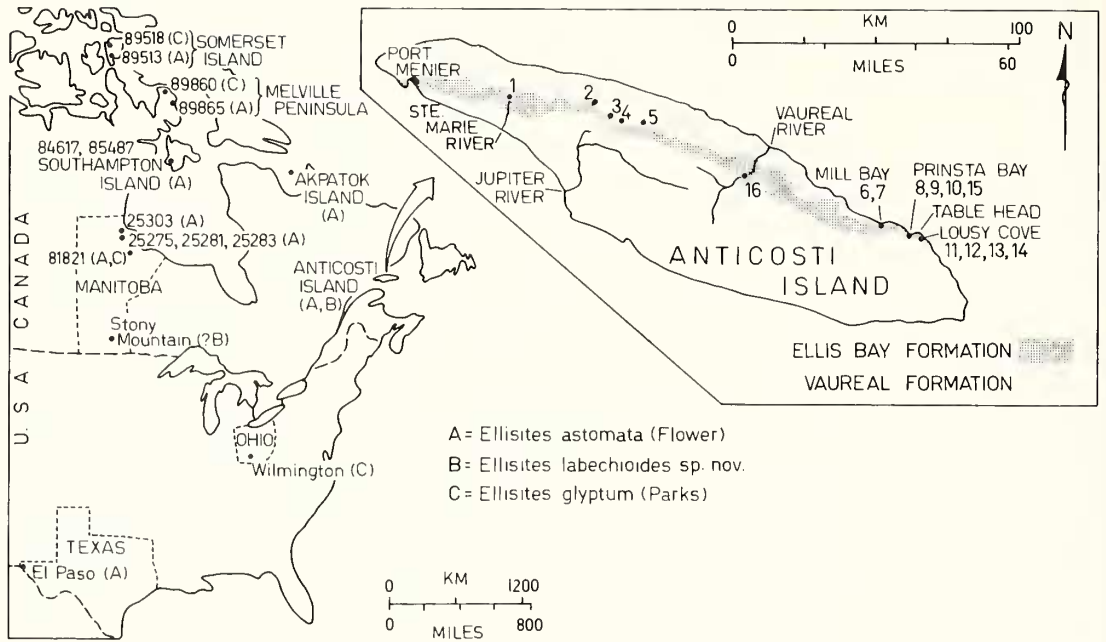
TEXT-FIG. 1. Map of North American occurrences of *Ellisites* gen. nov. Five-digit numbers denote Geological Survey of Canada (GSC) locality numbers. For locs. 1–16 in the upper Ordovician Vaureal and Ellis Bay formations of Anticosti Island, see Appendix.

SYSTEMATIC PALAEONTOLOGY

The repositories of the specimens quoted are denoted by the following abbreviations: GSC, Geological Survey of Canada, Ottawa; IU, Paleontology Collections, Indiana University, Bloomington; ROM, Royal Ontario Museum, Toronto; UM, Museum of Paleontology, University of Michigan, Ann Arbor; NMBM, New Mexico Bureau of Mines, Socorro.

Order HELIOLITIDA Frech, 1897
Suborder HELIOLITINA Frech, 1897
Superfamily COCCOSERIDICAE Kiaer, 1899

Diagnosis (emended after Hill 1981). Corallum encrusting, laminar or subglobular; longitudinal skeletal elements commonly greatly thickened and porous or aporose; horizontal skeletal elements thin and abundant to absent; tabularia with twelve contiguous septa composed of monacanths? (or rhabdacanths) directed upward adaxially; in some, septa long, thick, filling lumina; in some, septa short with flat tabulae present; in some, septa ill-defined, with vertical septal and axial trabeculae filling or partly filling lumina; coenenchyme of longitudinal trabeculae commonly so thick that no tubular lumina occur; in some, trabeculae outline tubules that may be crossed by subhorizontal diaphragms; in some, thick trabeculae combined with vesicular plates in coenenchyme and tabularia.

Family ELLISITIDAE fam. nov.

Diagnosis. Corallum incorporating vesicular transverse skeletal elements and aporose, pinnately fibrous, longitudinal skeletal elements.

Occurrence. Ashgill (Edenian to Gamachian) of North America.
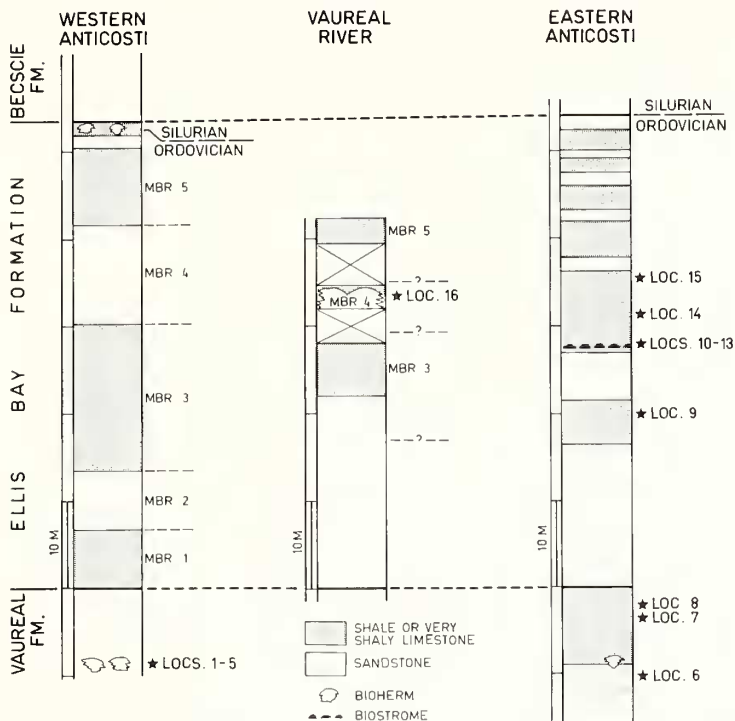
TEXT-FIG. 2. Stratigraphic setting of Anticosti Island collecting localities for *Ellisites* gen. nov. Western Anticosti and Vaureal River sections after McCracken and Barnes (1981, p. 62). Eastern Anticosti section based on unpublished data of P. Copper, from the Schmitt Creek–Mill Bay area (Vaureal Formation) and Table Head–Fox Point–Prinsta Bay area (Ellis Bay Formation). Limestones predominate in blank parts of the sections.

Genus ELLISITES gen. nov.

Name. From the Ellis Bay Formation, in which it occurs abundantly.

Diagnosis. Coenenchymal, septal, and axial trabeculae weakly differentiated, all vertical; tabularia outlined by rings of slightly larger trabeculae and filled by axial and septal trabeculae in zones of trabecular dilation; tabularia largely undefined in non-trabecular zones, may be represented by columns of incomplete tabulae merging with coenenchymal vesicles.

Contained species. Type species: *E. labechioides* sp. nov. from the Upper Ordovician (Ashgill) Vaureal and Ellis Bay formations of Anticosti Island and possibly Stony Mountain Formation, southern Manitoba (this paper).

   E. astomata (Flower, 1961) from the Upper Ordovician of Anticosti Island, Akpatok Island, Bray Island, north-eastern and southern Manitoba (this paper), and western Texas.

   E. glyptum (Parks, 1910) from the Upper Ordovician (Ashgill) of south-western Ohio, north-eastern Manitoba, Melville Peninsula, and Somerset Island.

Ellisites labechioides sp. nov.

Plate 30; Plate 31, figs. 1–3, 5 and 6; Plate 32, figs. 1 and 2; text-fig. 3A

v 1981   *Labechia* n. sp. aff. *L. mirabilis–L. banksi* group; Bolton, p. 42, pl. 1, fig. 4; pl. 2, figs. 1 and 2.

Derivation of name. Labechioides refers to the morphological likeness to labechiid stromatoporoids.

Type locality and horizon. Loc. 11: coastal tidal flat exposure (exposed at low tide) and bluffs to the west of Lousy Cove, north to Table Head, north-eastern Anticosti Island. Ellis Bay Formation: biostrome 0·5 m thick, enclosed by calcareous shale, situated 24·5–26·0 m below the Ellis Bay/Becscie formational boundary as defined by Cocks and Copper (1981).

Material, horizons, and localities. Holotype, nineteen paratypes, and numerous other specimens from Anticosti Island. Holotype, GSC 77880 (loc. 11), from Ellis Bay Formation. Paratypes from upper Vaureal Formation include: GSC 67013 and 77892 (loc. 3a), 67022 (loc. 3b), 77893 (loc. 3c), 67023 (loc. 4), and 77894 and 77895 (loc. 5). Paratypes from Ellis Bay Formation include: GSC 77881 (loc. 9), 77882 (loc. 10), 77883 (loc. 11), 77884 (loc. 15), and 67016, 77885–77891 (loc. 16). Other specimens from locs. 12, 13, and 14. Hypotype, GSC 77917, from Penitentiary Member, Stony Mountain Formation, Stony Mountain, southern Manitoba. Upper Ordovician (Richmondian-Gamachian).

Diagnosis. Ellisites with strongly vesicular coenenchyme and thin zones of short dilated trabeculae; trabeculae prismatic, 0·25–0·40 mm in diameter, composed of fibres diverging upward at 20–30° from vertical. Vesicles moderately convex, with width : height ratios of 2·4 : 1 to 2·8 : 1. Corallites weakly defined, 1·5–1·7 mm in diameter, with centres 1·8–2·2 mm apart.

Description. Most specimens from western and central Anticosti Island are laminar sheets with flat, broad domal, or cylindrical forms mimicking surfaces encrusted, some even irregularly nodose. Corallum thicknesses generally vary from 1·0–5·0 cm, and the largest specimen is 9·0 cm across, except at locality 4 where specimens up to 28·0 cm in diameter and 8·5 cm high have been collected from Vaureal Formation bioherms. The Ellis Bay Formation specimens from the north-east coast are mainly domal to rounded colonies, 15·0–20·0 cm in diameter and 10·0–15·0 cm high (maximum 24·0 cm diameter by 20·5 cm height). Each corallum has a thin basal epitheca less than 0·1 mm thick that parallels the substrate in minute detail (Pl. 30, fig. 1). The remainder of the corallum consists of two basic skeletal structures in different proportions in different growth zones: arched vesicles and vertical pillar-like trabeculae.

Vesicles generally predominate in the skeleton, particularly in juvenile parts (Pl. 30, fig. 1; Pl. 31, figs. 1 and 2). They are moderately convex with average width : height ratios generally between 2·4 : 1 and 2·8 : 1. Vesicle size varies considerably and this is particularly expressed in alternating growth zones (Pl. 30, fig. 6; Bolton 1981, pl. 1, fig. 4). 'Light' zones have average values for vesicle width : height (*apparent* dimensions, as measured in vertical section) between 0·5 : 0·2 mm and 0·75 : 0·35 mm in different specimens. The largest vesicles are up to 2·0 mm wide and 0·6 mm high and tend to occur toward the base of the corallum. Generally thinner 'dark' zones have vesicles one-half to one-third the size of those in the 'light' zones—width : height averages between 0·25 : 0·1 mm and 0·3 : 0·1 mm in different specimens. Convexity does not change consistently from one zone to another; more variation can be seen from one specimen to another than from zone to zone.

Short vertical trabecular rods are concentrated in 'dark' zones in juvenile parts of coralla and are usually more frequent and more pervasive in later growth stages (Pl. 30, figs. 1 and 4). They form thin layers 0·2–0·5 mm thick in which they are expanded laterally and commonly are in contact with adjacent trabeculae along part of their length. Their margins remain sharp and clear, and resulting polygonal prisms (Pl. 30, fig. 5; Pl. 31, fig. 3) average about 0·3 mm (range 0·25–0·4 mm) in diameter. The trabeculae consist of pinnately


EXPLANATION OF PLATE 30

Figs. 1–6. *Ellisites labechioides* gen. et sp. nov. from Anticosti Island.   1, paratype, GSC 77885, loc. 16, Ellis Bay Formation, member 4; longitudinal section showing encrusting basal epitheca, and astogenetic change from mainly vesicular (below) to mainly trabecular (above); upper surface extensively bored, × 5.   2, paratype, GSC 77882, loc. 10, Ellis Bay Formation; exterior surface with sediment-filled calices surrounded by rings of papillae (ends of trabeculae), × 9.   3, paratype, GSC 67023, loc. 4, upper Vaureal Formation; longitudinal section showing column of broader vesicles (tabulae) bordered by smaller vesicles (coenenchyme), × 10.   4, paratype, GSC 77887, loc. 16, Ellis Bay Formation, member 4; longitudinal section showing characteristic V–shaped arrangement of fibres in trabeculae, × 10.   5, 6, holotype, GSC 77880, loc. 11, Ellis Bay Formation; tangential section (5) showing zone of fully dilated prismatic trabeculae (upper right) between zones mainly of vesicular plates, and longitudinal section (6) with zones of smaller vesicles and isolated trabeculae alternating with zones of larger vesicles mostly free of trabeculae, both × 10.

PLATE 30

DIXON, BOLTON and COPPER, *Ellisites*
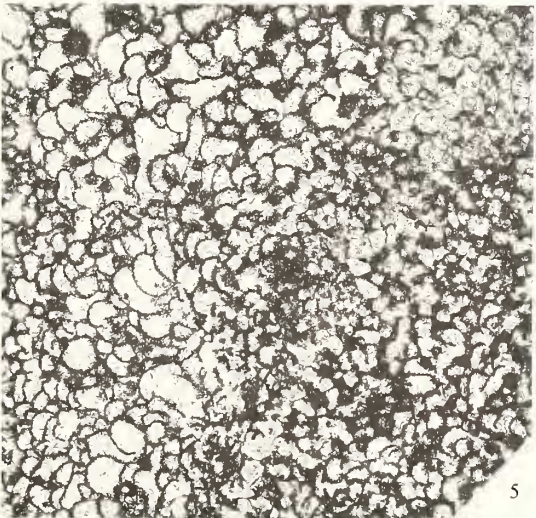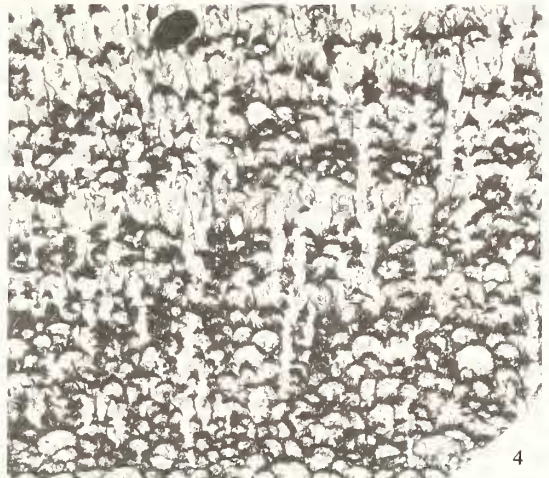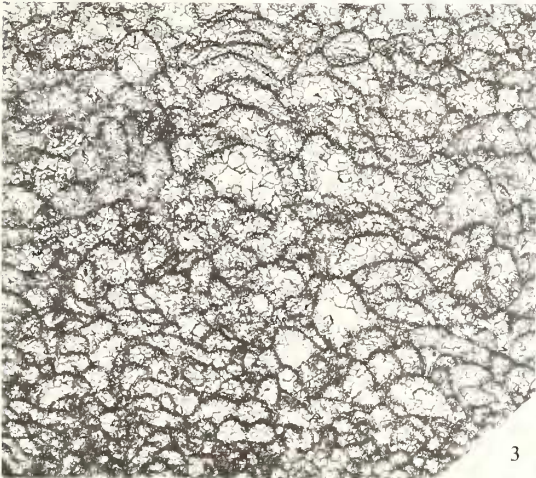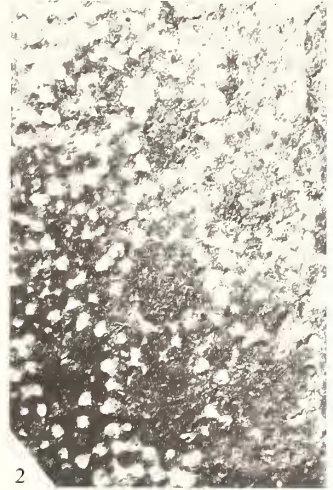
arranged calcite fibres diverging upward at 20–30° from the axes of trabeculae (Pl. 30, fig. 4; Pl. 31, fig. 5). In later parts of the corallum where trabecular zones are more crowded, some trabeculae continue from one zone to the next and reach lengths up to 3·5 mm. Trabeculae have acute to rounded terminations at the top, and longer ones pinch and swell in penetrating 'light' and 'dark' zones respectively, but the lateral extensions do not coincide with associated vesicle margins as in the swelling pillars of *Labechia* (e.g. *L. venusta* Yavorsky, 1955 *in* Nestor 1966, pl. 2, fig. 1). A few short isolated trabeculae occur in 'light' zones and in some specimens trabeculae are so weakly developed in 'dark' zones that they remain as isolated short spindle-shaped or longer tapering rods concentrated at particular levels (Pl. 31, figs. 2 and 6). Growth of trabeculae was generally initiated on arched upper surfaces of vesicles (Pl. 31, fig. 5). Some are shorter than the vaulted spaces beneath vesicles; others penetrate one or more vesicles vertically. Both penetration of vesicles by trabeculae and, conversely, interruption of vertically aligned trabeculae by complete vesicles are common. The latter, however, is probably only apparent and can result commonly from the plane of section being parallel to, but slightly offset from, the axes of trabeculae that pinch and swell along their length.

The coenosteum contains corallites that are most clearly shown by calices on the exteriors of several specimens (Pl. 30, fig. 2; Pl. 32, fig. 1) but can rarely be discerned in transverse sections of most specimens. Where sections are cut tangential to the upper surfaces of zones of dilated trabeculae, corallite walls are defined by regularly disposed rings of contiguous trabeculae surrounding clusters of axial trabeculae that appear smaller and separated because they are intersected nearer their narrow terminations (text-fig. 3A). Each ring comprises thirteen to sixteen trabeculae, some slightly elongate radially; the latter are suggestive
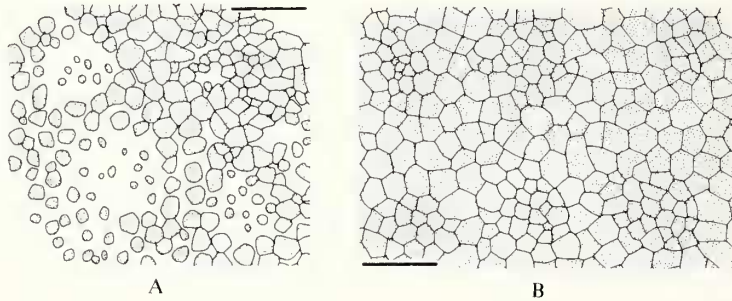

TEXT-FIG. 3. A, *Ellisites labechioides* gen. et sp. nov.; paratype, GSC 77894, from upper Vaureal Formation, loc. 5, Anticosti Island. Tracing of tangential section near upper surface of trabecular zone. Corallites shown by clusters of isolated smaller (axial) trabeculae surrounded by larger (septal, coenchymal) trabeculae. See also Plate 31, fig. 3. B, *E. astomata* (Flower); hypotype, GSC 77900, from upper Vaureal Formation, loc. 3c, Anticosti Island. Tracing of tangential section showing clusters of smaller trabeculae in corallite centres, surrounded by larger trabeculae. See also Plate 34, fig. 1. Scale bars 1·0 mm.

EXPLANATION OF PLATE 31

Figs. 1–3, 5, 6. *Ellisites labechioides* gen. et sp. nov. from Anticosti Island. 1, 2, paratype GSC 77886, loc. 16, Ellis Bay Formation, member 4; tangential (1) and longitudinal (2) sections through zones mainly of vesicular plates, with a thin zone of small vesicles with isolated trabeculae in fig. 2, × 10. 3, paratype GSC 77894, loc. 5, upper Vaureal Formation; tangential section, × 10 (compare with text-fig. 3). 5, paratype, GSC 77889, loc. 16, Ellis Bay Formation, member 4; longitudinal section showing trabeculae initiated on upper surfaces of vesicles and penetrating subsequent vesicles, × 20. 6, paratype, GSC 77888, loc. 16, Ellis Bay Formation, member 4; tangential section showing a zone of isolated rounded trabeculae and a non-trabeculate vesicular zone, × 10.

Fig. 4. Coccoserid *Dualites? speleana* (Hill). GSC 77918, Fossil Hill, west of Mandurama, New South Wales, Kalimna Limestone Member of Fossil Hill Limestone; longitudinal section showing upwardly converging septal trabeculae, × 10.

PLATE 31

DIXON, BOLTON and COPPER, *Ellisites*
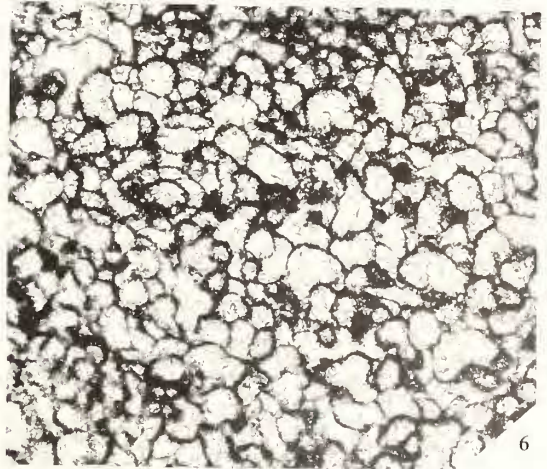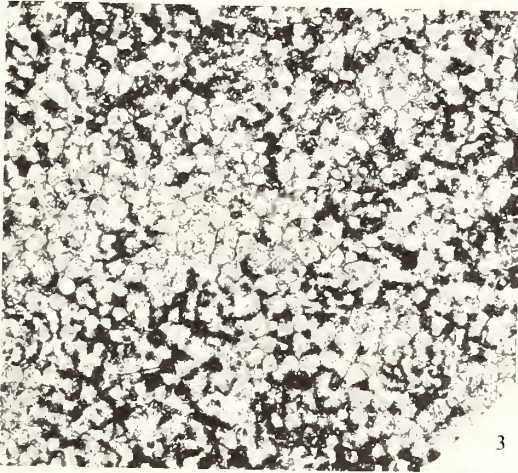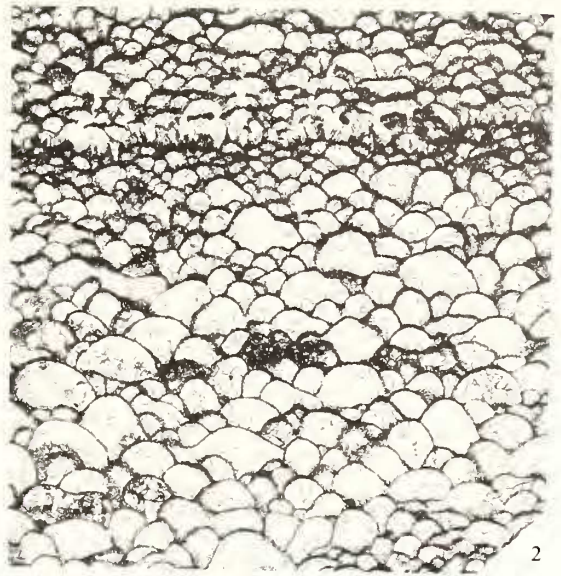
of septal trabeculae but the twelvefold septal pattern typical of heliolitids is at best obscure. In longitudinal section there is no clear indication of inclined trabeculae that might represent septa.

Corallites average 1·5–1·7 mm in diameter (outside the ring of trabeculae) and have calices about 1·2–1·4 mm in diameter. Their centres are spaced 1·8–2·2 mm apart, corresponding to numbers of corallites ranging from eighteen to thirty-six per cm² in cross-section. Corallites are indistinguishable in zones of full dilation of trabeculae: a uniform array of polygonal prisms belies the presence of corallites and of coenenchymal, septal, and axial trabeculae. Corallites are, at most, vaguely expressed in vesicular zones. Longitudinal sections of some specimens show slight but repeated depressions in the layers of vesicles. Beneath these depressions are indistinctly bounded columns of slightly larger vesicles incorporating marginal ones that dip gently into the depression and inosculate with axial vesicles that are horizontally based. In several specimens (e.g. Pl. 30, fig. 3; Pl. 32, fig. 2), where these minor depressions are not expressed, smaller and larger vesicles are very weakly segregated into columns, with larger vesicles in columns of a size and spacing comparable to corallite size and spacing in trabecular zones. If these columns of larger vesicles represent corallites, then the vesicular incomplete tabulae represented are usually scarcely distinguishable from horizontally based coenenchymal vesicles.

Discussion. *E. labechioides* sp. nov. differs from the other species on Anticosti Island, *E. astomata*, in having a predominantly vesicular coenosteum with only thin zones of short trabeculae, and in having the pinnate trabecular fibres consistently much more narrowly divergent upwards. It differs for similar reasons from Melville Peninsula specimens referred by Bolton (1977, p. 29, pl. 3) to *Coccoseris astomata* Flower. Relationships and similarities are discussed further below. The southern Manitoba specimen (GSC 77917) varies in that the trabecular fibres are more broadly divergent, more like *E. astomata*.

<center>*Ellisites astomata* (Flower, 1961)</center>

<center>Plate 32, figs. 3–7; Plate 33; Plate 34, fig. 1; text-fig. 3b</center>

1961   *Coccoseris astomata* Flower, pp. 56–57, pls. 16–18.
v 1975   *Coccoseris astomata* Flower; Dixon, p. 176 (*pars*).
v 1975   stromatoporoids, Cumming, p. 38 (*pars*).
v 1975   *Coccoseris* cf. *C. astomata* Flower; Norford *in* Trettin, p. 49.
v 1976   *Coccoseris astomata* Flower; Bolton *in* Workum *et al.*, p. 170, pl. 1, figs. 5 and 6.
v 1977   *Coccoseris astomata* Flower; Bolton (*pars*), p. 29, pl. 3, figs. 2, 3, 5; *non* pl. 3, figs. 1 and 4.

Type locality and horizon. Holotype, NMBM 670, is from near the crest of Scenic Drive, El Paso, Texas. Second Value Formation, Montoya Group; Edenian–lower Maysvillian.

<center>EXPLANATION OF PLATE 32</center>

Figs. 1 and 2. *Ellisites labechioides* gen. et sp. nov. Paratype, GSC 77895, loc. 5, Anticosti Island, upper Vaureal Formation. 1, exterior surface showing corallite calices, × 5. 2, longitudinal section through mostly vesicular coenosteum with very thin zones of trabeculae and smaller vesicles; vesicles are in vaguely defined columns, with larger ones (apparently tabulae in corallites) segregated from somewhat smaller ones (dissepiments in coenenchyme, appearing slightly darker on photograph), × 5.

Figs. 3–7. *E. astomata* (Flower) from Anticosti Island, upper Vaureal Formation. 3, 4, hypotype, GSC 77901, loc. 5, longitudinal section (3) showing growth interruptions: trabeculae to right terminate beneath a thin zone of fibro-normal calcite that forms a base for succeeding vesicular plates while trabeculae to left continue across horizon of interrupted growth, × 10; exterior surface (4) showing corallite calices as clusters of smaller papillae (axial trabeculae) in slight depressions, surrounded by larger papillae (?septal and coenenchymal trabeculae), × 5. 5, 7, hypotype, GSC 77902, loc. 5; tangential section (5) of a thin zone of trabeculae showing their initiation on vesicular plates (below), expansion to contiguity (centre), and acute terminations (top left), × 10; longitudinal section (7) of alternating vesicular and thin trabecular zones in the lower part of a colony, and the base of an overlying entirely trabecular zone, × 10. 6, hypotype, GSC 77899, loc. 3c; longitudinal section of specimen with nodular growth surfaces and marked growth zonation; nodes are underlain by pillars of continuous trabecular construction while intervening depressions show alternating thin trabecular layers and thicker lenses of vesicular plates, × 4.

PLATE 32

DIXON, BOLTON and COPPER, *Ellisites*
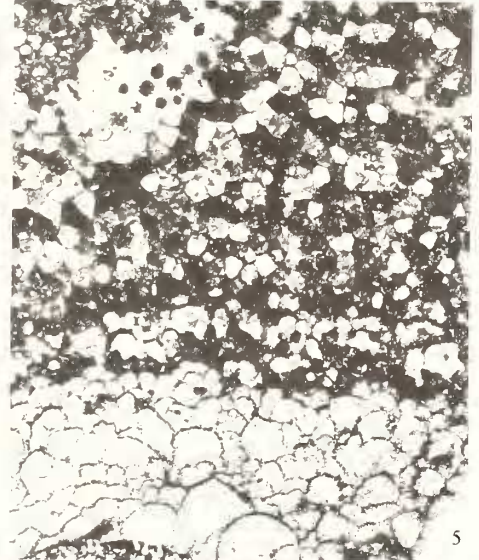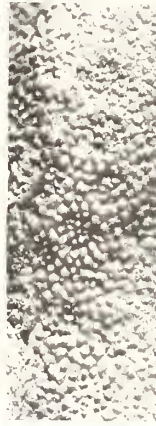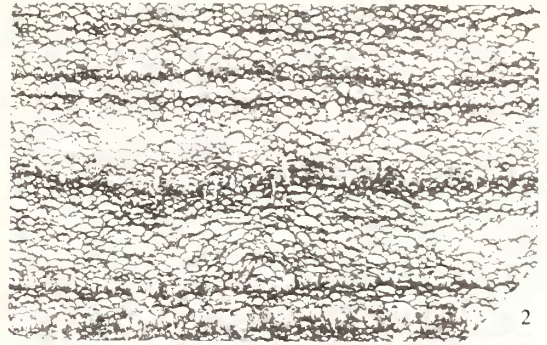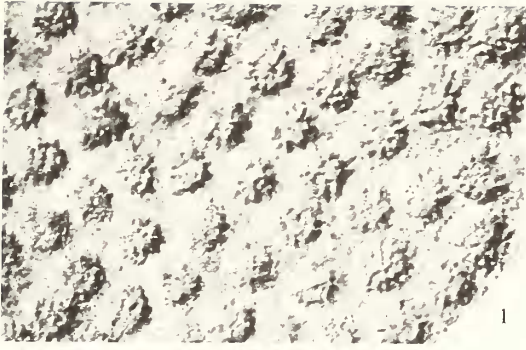
Material, horizons, and localities. Nine hypotypes and other specimens from the Upper Ordovician (Richmondian) upper Vaureal Formation of Anticosti Island: GSC 77896 (loc. 1), 77897 (loc. 2 = GSC loc. 36269), 77898 (loc. 3a = GSC loc. 36146), 77899 and 77900 (loc. 3c = GSC loc. 76087), 77901 and 77902 (loc. 5), 77903 (loc. 6), and 77904 (loc. 8). Other specimens from loc. 7. Fifteen hypotypes from other localities: Upper Ordovician (Edenian) Bad Cache Rapids Formation, Melville Peninsula, GSC 42920 and 42921 (GSC loc. 89865); Upper Ordovician (Edenian) Baillarge/Bad Cache Rapids Formation, Bray Island, GSC 78027 (GSC loc. C-2845); Upper Ordovician (Edenian) beds, Akpatok Island, GSC 41177; Upper Ordovician (Edenian–Maysvillian) Thumb Mountain Formation, Somerset Island, GSC 77905 (GSC loc. 89513); Upper Ordovician (Edenian–Maysvillian) Bad Cache Rapids Group—Portage Chute Formation, Churchill River, GSC 77919 (GSC loc. 25275); Upper Ordovician (Richmondian) Churchill River Group—Caution Creek Formation, South Knife River, GSC 77907 (GSC loc. 25303) and mouth of Chasm Creek, GSC 77908 (GSC loc. 25281), Chasm Creek Formation, member 1, mouth of Chasm Creek, GSC 77909–77911 (GSC loc. 25281), and Churchill River, GSC 77912 (GSC loc. 25283), and Angling River, GSC 77906 (GSC loc. 81821), north-eastern Manitoba; Upper Ordovician (Edenian) Bad Cache Rapids Group, 0·6 km west of Coral Harbour, Southampton Island, GSC 77913, and 77914 (GSC locs. 84617 and 85487).

Diagnosis. Ellisites with thick zones of fully dilated trabeculae and subordinate sectors of vesicular coenosteum or, rarely, with vesicles obscure; trabeculae prismatic, 0·2–0·45 mm in diameter, composed of fibres diverging upward at 50–60° from vertical, vesicles moderately convex, with width : height ratios of 2·1 : 1 to 2·5 : 1; corallites obscure, 1·5–1·9 mm in diameter, with centres 1·6–2·3 mm apart.

Description. Five of the Anticosti Island hypotypes are parts of lamellar sheets up to 3·5 cm thick and 10·0 cm wide, and a sixth and seventh are upwardly expanding domal forms up to 4·5 cm high and 8·0 cm across. A thin basal epitheca defines the base of the colony and is intimately moulded to the surface of the encrusted substrate. The remainder of the corallum is constructed of arched vesicles and strongly dilated vertical trabeculae in fairly discrete growth zones.

A vesicular zone typically follows the basal epitheca and other vesicular sectors occur in trabecular zones higher in the colony (Pl. 32, figs. 3 and 6). Vesicles are moderately convex with average width : height ratios between 2·1 : 1 and 2·5 : 1. Average width : height values (*apparent* values, as measured in longitudinal section) range from 0·55 : 0·25 mm to 0·75 : 0·3 mm in different specimens. Vesicles attain maximum widths of 1·5 mm and heights of 0·9 mm, usually in the basal zone of a corallum. Vesicular zones tend to be discontinuous laterally, mainly forming lens- or wedge-shaped sectors that fill substrate and colony surface irregularities (Pl. 32, figs. 3 and 6). Vesicles are obscure in some specimens and were not recorded in the holotype (Flower 1961, pp. 56–57).

Zones of strongly dilated vertical trabeculae up to 15 mm thick form the bulk of the corallum in these specimens. The trabeculae either arise as discrete pillars directly from the surface of a layer of vesicles (Pl. 33, fig. 5) or are rooted in an initial thin layer of fibro-normal calcite covering a layer of vesicles (Pl. 32, fig. 3; Pl. 33, fig. 6). The trabeculae typically expand abruptly to contiguity with adjacent trabeculae (Pl. 32, fig. 7; Pl. 33, fig. 5) and remain fully dilated for most of their length. In the main trabecular zones they form sub-parallel, vertical, polygonal prisms only locally interrupted by vesicular plates in discontinuous layers one or a few vesicles thick (Pl. 32, fig. 3). The prisms average 0·3–0·35 mm in diameter (range 0·2–0·45 mm), and

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EXPLANATION OF PLATE 33

Figs. 1–6. *Ellisites astomata* (Flower). 1, hypotype, GSC 77913, GSC loc. 84617, Southampton Island, Bad Cache Rapids Formation; tangential section showing mostly contiguous prismatic trabeculae with well-preserved fibrous microstructure, × 10. 2, 3, hypotype, GSC 77914, GSC loc. 85487, Southampton Island, Bad Cache Rapids Formation; longitudinal (2) and tangential (3) sections showing fully dilated prismatic trabeculae with fibrous microstructure (note diagenetic loss of some microstructure in fig. 3, compared to fig. 1), × 10. 4, hypotype, GSC 77904, loc. 8, Anticosti Island, upper Vaureal Formation; tangential section with prismatic trabecular skeleton (lower area) and vesicular sector penetrated by isolated rounded papillae (ends of trabeculae), × 20. 5, 6, hypotype, GSC 77906, GSC loc. 81821, Angling River, north-eastern Manitoba, Chasm Creek Formation; longitudinal sections showing sectors of vesicular plates interrupting prismatic trabeculae (5), × 10; and a sector of vesicular plates penetrated by papillate ends of trabeculae in the same corallum (6), × 20.

PLATE 33
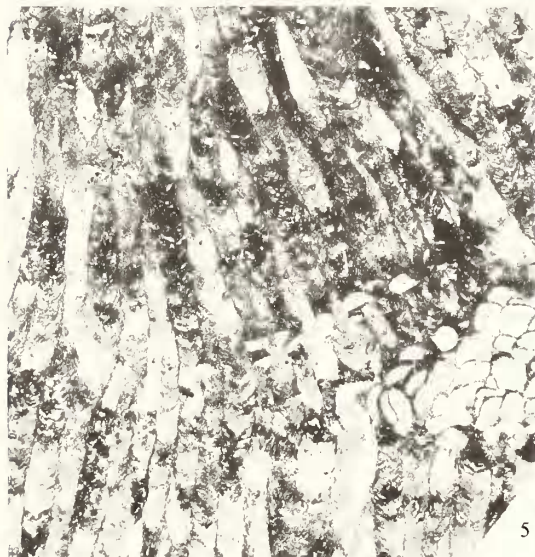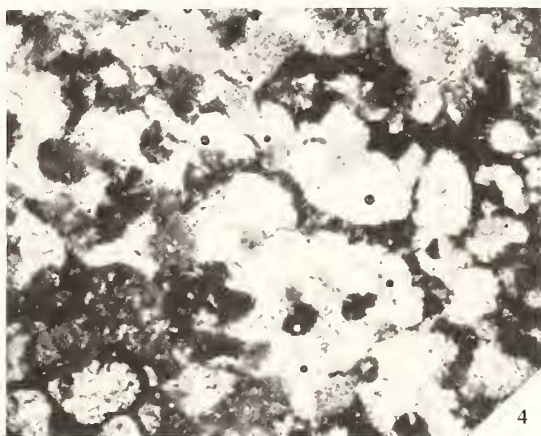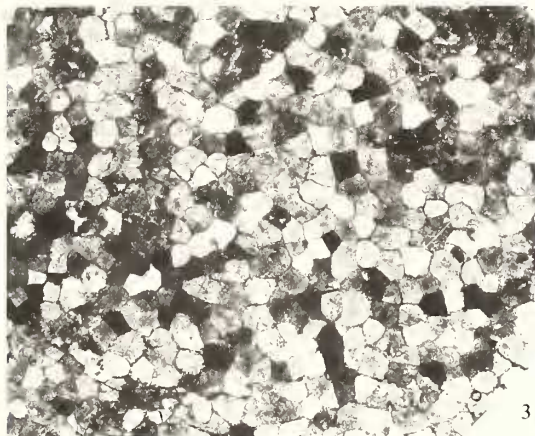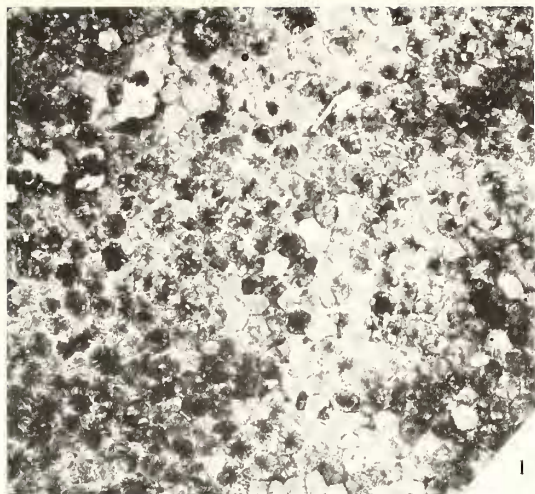
DIXON, BOLTON and COPPER, *Ellisites*

terminate as acute papillae at the top (Pl. 32, fig. 6; Pl. 33, figs. 4 and 5). They consist of pinnately arranged calcite fibres diverging upward at angles of 50–60° from the axes of trabeculae (Pl. 33, figs. 2 and 5). Both V and U-shaped arrangements of fibres are evident in longitudinal sections; the former is shown where trabeculae are cut along their axes, the latter in trabeculae cut parallel to their axes but off-centre.

Short conical denticle-like structures are scattered through vesicular sectors (Pl. 32, figs. 5 and 7), a few rising from the surface of any one vesicle and not reaching the vesicle above. Similar short denticles arise from thin fibro-normal layers resting locally directly on the basal epitheca. These denticles appear to represent trabeculae that were 'aborted' without developing into zones of fully dilated prisms. Some of these short denticles show the distinctive trabecular pinnate fibrous structure, while others are composed of dark granular calcite. The differences are attributed to recrystallization, as similar variations can be seen both within the thin layers of fibro-normal calcite and from one trabecular prism to another in the principal layers (Pl. 32, fig. 3; Pl. 33, figs. 2 and 3); all are interpreted as originally of fibrous structure.

The presence of corallites can be detected with certainty as calices on the upper surfaces of several specimens (e.g. Pl. 32, fig. 4). Corallites appear to be differentiated clearly only at the upper surfaces of layers of trabecular prisms where the trabeculae terminate in small acute papillae. The latter are readily reduced by abrasion to tubercle-like form and calice walls become defined by rings of larger tubercles enclosing slightly depressed axial clusters of smaller ones (Pl. 32, fig. 4). None of the tubercles in a ring is distinctly elongate radially, analogous to radial elongation of septal trabeculae in some other coccoserids. In two specimens corallite diameters are 1·5 and 1·9 mm, calice diameters 1·1 and 1·5 mm, and corallite centres average 1·6 and 2·3 mm apart.

In transverse section the trabecular prisms appear as a mosaic of sharply delimited polygons with little suggestion of corallite structure (Pl. 33, figs. 1 and 3). One specimen from Anticosti Island (text-fig. 3B) shows numerous clusters of six to twelve generally smaller trabeculae (∼0·2 mm diameter) surrounded by larger ones (∼0·35 mm diameter). The clusters are ill-defined but their centres average about 1·9 mm apart (based on seventy measurements), i.e. distances of the same order as the spacing of corallites on other specimens. Another specimen from Akpatok Island (Pl. 34, fig. 1) is similar. No other indication of corallite structure has been recognized in transverse sections.

In longitudinal section the trabecular prisms are uniformly vertical with no indication of inclination such as seen in septal trabeculae of many coccoserids. No trace of corallite structure is evident in sectors of vesicular plates.

Discussion. This species differs from *E. labechioides* sp. nov. in having a coenosteum composed predominantly of thick zones of contiguous vertical trabeculae, vesicular plates mostly in discontinuous sectors, and trabeculae with pinnate fibres consistently more broadly divergent upward.

Flower (1961, pp. 56–57) considered his holotype of *C. astomata* from the late Edenian–early Maysvillian Second Value Formation of western Texas to be anomalous (for a heliolitid coral) in showing no clear evidence of corallites, merely slight and obscure variations in size and aspect of the trabeculae. Corallites are certainly obscure in *E. astomata* but are evident as calices on some well-preserved surfaces of specimens from Anticosti Island (Pl. 32, fig. 4), north-eastern Manitoba, and Southampton Island, and are suggested internally on three specimens by ill-defined but appropriately spaced clusters of small trabeculae enclosed by slightly larger ones (Pl. 34, fig. 1; text-fig. 3B).

Flower's holotype compares closely with all the material ascribed to *E. astomata* in this paper, except in one character. Vesicular plates are not mentioned in Flower's description, nor are any evident in the excellent accompanying photographs (ibid., pls. 16–18) of the well-preserved specimen. However, the Canadian specimens studied vary in this regard. Many from Anticosti Island have conspicuous vesicular sectors; others from there and elsewhere (see below) have only minor or obscure vesicles. The repetition of vesicular sectors is evidently astogenetic and probably reflects environmentally induced growth variations. The holotype is interpreted, therefore, to be an anomalous representative of a species that occurs widely in North America but that usually possesses some vesicular skeletal plates.

An encrusting form (GSC 41177) assigned to *C. astomata* from the Edenian beds of Akpatok Island, with trabeculae 0·20–0·24 mm (range 0·14–0·44 mm) in diameter, displays minute basal vesicles; a similarity to *Dermatostroma? escanabaense* was noted (Bolton *in* Workum *et al.* 1976,

p. 170, pl. 1, fig. 6). The specimen is here included in *E. astomata*. Bolton (1977, p. 29, pl. 3, figs. 1–5) referred fossils from the lower Upper Ordovician (Edenian) Bad Cache Rapids Formation of Melville Peninsula to *C. astomata*. These specimens too have prismatic trabeculae with broadly divergent fibres characteristic of Flower's species. Significantly, they also have local basal sectors of vesicular plates ('. . . suggesting a stromatoporoid affinity for the species'—Bolton 1977, p. 29) as in the Anticosti Island specimens of *E. astomata*. Among the Melville Peninsula specimens, two hypotypes (GSC 42920, 42921) have smaller trabeculae (diameters of 0·25–0·45 mm) than the third (diameters of 0·75–0·9 mm). In the context of the Anticosti Island material the former closely resemble *E. astomata*; the latter is not represented. A domal colony (GSC 78027) from the Edenian Baillarge/Bad Cache Rapids Formation of Bray Island, Foxe Basin (Trettin 1975, p. 49) has trabeculae 0·24–0·4 mm in diameter and in the sections prepared has no clearly developed vesicles. It is assigned to *E. astomata* and is one of the specimens showing clusters of small trabeculae (presumably within corallites) surrounded by slightly larger ones. One specimen (GSC 77905) listed as *C. astomata* by Dixon (1975, p. 176) from the Edenian–Maysvillian Thumb Mountain Formation of Creswell Bay, Somerset Island (GSC loc. 89513) has trabeculae 0·28–0·40 mm in diameter, with rare basal vesicles, and is consistent with the Anticosti Island forms of *E. astomata*. Similarly, one laminar colony (GSC 77906; Pl. 33, fig. 5) collected from the Richmondian Chasm Creek Formation, Churchill River Group, of the Nelson–Angling rivers area, north-eastern Manitoba (Cumming 1975, p. 38; GSC loc. 81821), has trabeculae averaging 0·32 mm (range 0·24–0·48 mm) in diameter with vesicular areas at various levels identical to the Anticosti Island forms of *E. astomata*. A thin laminar colony (GSC 40949), collected from the Maysvillian–Richmondian Mount Kindle Formation, Mount Kindle, Franklin Mountains, District of Mackenzie (Norford and Macqueen 1975; GSC loc. 69793), has poorly preserved trabeculae ranging from 0·16 to 0·40 mm in diameter with no vesicular areas, and is questionably referred to *E. astomata*. Relationships and similarities are discussed more fully below.

SEDIMENTARY AND PALAEOENVIRONMENTAL ASSOCIATIONS

The best evidence of lithological and palaeoenvironmental setting is from the coastal exposures of north-eastern Anticosti Island (locs. 6–15); most collecting localities inland are isolated bedding plane exposures or isolated exposures of more resistant biohermal/biostromal limestone that provide less information on prevailing depositional environments.

Generally colonies are small and scarce in the upper Vaureal Formation. *E. labechioides* and *E. astomata* occur together in the Vaureal Formation in a bioherm (loc. 3c) and in biostromal nodular lime mudstone (loc. 5) rich in *Palaeophyllum*, tabulate corals (*Calapoecia*, *Paleofavosites*, *Catenipora*, *Propora*, and others), and aulacerid stromatoporoids. *E. astomata* alone has been collected from other Vaureal Formation bioherms (loc. 1) along with abundant *Paleofavosites* and common *Palaeophyllum*, *Calapoecia*, and aulacerid stromatoporoids. In the north-eastern exposures it is commonly associated with very large *Paleofavosites* colonies in both argillaceous calcarenite (loc. 6) and nodular grey calcareous shale with thin calcarenite interbeds (locs. 7 and 8).

Ellisites is most abundant, largest, and best developed in the lower–middle Ellis Bay Formation. *E. labechioides* occurs in profusion in the Table Head Creek–Prinsta Bay sections of the lower–middle Ellis Bay Formation (locs. 10–13). In one biostrome, tabulate corals (favositids, heliolitids) and aulacerid stromatoporoids are packed in a calcareous shale matrix and the biostrome is underlain and overlain by thin-bedded limestone and dark calcareous shale. The species also occurs in soft calcareous shale (locs. 9, 14, 15) along with abundant tabulate corals and aulacerids. In its highest stratigraphic occurrence it occurs in both a bioherm and its capping shale (loc. 16), together with abundant large *Palaeophyllum*, *Paleofavosites*, stromatoporoids, and common smaller tabulates (*Propora* and *Catenipora*).

The majority of specimens, therefore, occur in argillaceous sediments or in sequences in which shales predominate (text-fig. 2). The association suggests mainly turbid, low energy, marine shelf environments with a substantial influx of fine terrigenous clastics. The environments represented

through the upper Vaureal and lower-middle Ellis Bay formations on eastern Anticosti Island were shallow enough, however, to be strongly agitated periodically. Terrigenous silt and quartz sand were introduced and trough cross bedding is conspicuous in sandstone and associated calcarenite beds within the predominantly argillaceous succession. Some coral and stromatoporoid colonies show evidence of being rolled or damaged; some recovered partially and resumed growth; some are incorporated in channel-fill sandstones.

Ellisites is commonly associated with other corals and stromatoporoids and evidently successfully exploited their skeletons as substrates for support. Roughly estimated, up to 40% of the *Ellisites* in the Ellis Bay Formation encrusted aulacerid stromatoporoids, up to 10% encrusted the tabulate coral *Calapoecia*, and the remainder grew either directly on sea-floor sediments or on objects that are no longer attached. They show evidence both of directly encrusting hard substrates and of expanding laterally over, and intertonguing with, loose sediment.

THE COCCOSERID-PROPORID CONNECTION

The three superfamilies of the Suborder Heliolitina Frech, 1897, have been distinguished largely by the nature of their coenenchyme (Hill 1981, p. F602). The Helioliticae Lindström, 1876, are characterized by open vertical diaphragmated tubules; the Proporicae Sokolov, 1949, by dissepiment-like plates; and the Coccoseridicae Kiaer, 1899 (= Protaraeida Bondarenko, 1967), by thick clinogonally fibrous longitudinal trabeculae.

The Anticosti Island corals described here do not fit unequivocally into any one of these groups as presently recognized. Their coenosteum is, however, most allied to that of the Coccoseridicae in having longitudinal skeletal elements (monacanthine trabeculae) greatly thickened, both as fully dilated longitudinal trabeculae in the coenenchyme and as upwardly directed trabeculae completely filling tabularia. The group differs from previously known Coccoseridicae in combining this distinctive trabecular structure with substantial zones or sectors of vesicular plates, the latter much resembling the coenenchyme of Proporicae. The obscurity of corallites in zones of vesicular plates is, however, a distinct difference from the Proporicae, in which corallites consistently have clearly defined walls. The group is therefore placed in the Coccoseridicae and considered to include early heliolitinid corals with characters suggesting a direct relationship between the Coccoseridicae and Proporicae. It conveniently forms the connection sought by Nestor (1981, pp. 24–25) who commented that '. . . phylogenetic relationships between the trabecular and cystose heliolitids are more obscure, as evidence of the existence of transitory forms between Protaraeida and Proporida is lacking'.

CLOSE RELATIONSHIPS

Related genera

Ellisites appears to be most closely related to forms variously assigned to *Coccoseris* Eichwald, 1855, or *Protaraea* Milne-Edwards and Haime, 1851. Whether *Coccoseris* and *Protaraea* are synonymous or are distinct genera has long been argued in the literature. Recently both Bondarenko (1980) and Sokolov and Tesakov (1984) contributed to the discussion by re-examining lectotype material of *C. ungerni* Eichwald and reassessing it in the context of available literature. Bondarenko recognized *Coccoseris* as a valid genus; Sokolov and Tesakov concluded that *Coccoseris* is a junior synonym of *Protaraea*. The latter authors contended that Milne-Edwards and Haime's description of the Richmondian material defining their new genus *Protaraea* does not conform to the description of the designated type species, the Trentonian *Porites? vetustus* Hall, 1847. They considered that the latter belongs either to *Esthonia* or to a new genus, and that Milne-Edwards and Haime's genotypic material more likely belongs, as indicated earlier by Foerste (1909), to *Protaraea richmondensis* Foerste, 1909. The problem may not be resolved further without complementary re-examination of the type material of Hall (1847) and Milne-Edwards and Haime (1851), as suggested by Hill (1981, p. F622).

As interpreted by Sokolov and Tesakov (1984), *Protaraea* (= *Coccoseris*) is characterized by a skeleton composed entirely of contiguous trabeculae, with corallites distinguishable only as calices on the surfaces of colonies. The only two species they considered clearly distinguishable differed from each other in arrangement of septal trabeculae and spacing of corallites: *P. ungerni* has vertical septal trabeculae and more widely spaced corallites, and *P. richmondensis* has inclined septal trabeculae and more closely spaced corallites. They considered at least eight other named species to be questionable pending further study. In contrast, Bondarenko (1980) regarded *Coccoseris* as a genus with closely spaced corallites and with entirely vertically arranged septal baculi (trabeculae) differentiated from axial and coenenchymal trabeculae on well-preserved external surfaces. The only other coccoserid with solely vertically oriented trabeculae was included in a new genus, *Neotumularia* Bondarenko, characterized by widely separated corallites and axial trabeculae markedly inhomogeneous in size. *Neotumularia* also lacks vesicular skeletal plates. *Dualites* Bondarenko, 1980, with closely spaced corallites, and *Micrastites* Bondarenko, 1980, with distant corallites, both have septal trabeculae inclined rather than vertical, and neither was reported to have vesicular skeletal plates. Plate 31, fig. 4 and text-fig. 4 represent a specimen (GSC 77918) from the late Early to early Middle Caradoc Cliefden Caves Limestone Group (Kalimna Limestone Member, Fossil Hill Limestone: Webby and Packham 1982, p. 306; Webby and Kruse 1984, p. 165) of New South Wales that may equate with what Bondarenko (1980, p. 111) designated *D.* (?) *speleana* (formerly *C. speleanus* Hill, 1957). The transverse and longitudinal sections display the characteristic appearance of inclined septal trabeculae; no transverse or longitudinal sections of *Ellisites* showed any such indication of inclined trabeculae. Very rarely a well-preserved exterior surface of *Ellisites* shows a few small radiate markings (Pl. 34, fig. 3) reminiscent of the crude septal pattern seen in the transverse section of *Dualites*.

Sokolov and Tesakov (1984) considered that *C. astomata* Flower belongs 'beyond all shadow of doubt' to *P. ungerni* as both have striking features in common: all trabeculae are vertically arranged and contiguous, and in consequence corallites are distinguishable only as calices on the surfaces of corallites. Forms herein assigned to *E. astomata* are clearly most similar to *P. ungerni* in the character of the trabecular skeleton but, importantly, all the North American material (except for Flower's) has vesicular skeletal elements which are not reported in *P. ungerni*. Ultimately, topotypic material of Flower's *C. astomata* should be examined to see if the absence of vesicular skeletal

TEXT-FIG. 4. Coccoserid *Dualites*? *speleana* (Hill). GSC 77918, Fossil Hill, west of Mandurama, New South Wales; Kalimna Limestone Member of Fossil Hill Limestone. Tangential section showing the radial pattern produced by inclined septal trabeculae, × 10. See also Plate 31, fig. 4 and Plate 34, fig. 3.

plates is consistent in the Texas species. If such is the case, then all the other North American specimens herein assigned to *E. astomata* would more appropriately be considered a new species of *Ellisites*.

Flower (1961, p. 57) commented on the superficial resemblance of *C. astomata* to a stromatoporoid. Of specimens herein referred to *Ellisites*, the first to be described were originally included in the stromatoporoid genera *Labechia* Milne-Edwards and Haime, 1851 (by Foerste 1910), and *Dermatostroma* Parks, 1910. *D. corrugatum* Parks, 1910 and *D. glyptum* Parks, 1910 from Ohio, and *D.? escanabaense* Galloway and Ehlers, 1961, from Michigan, all have a skeleton made up solely of contiguous prisms of fibrous calcite indistinguishable in character from zones of prismatic trabeculae in Anticosti Island *Ellisites*. The uncertain systematic position of these three species has long been recognized. Galloway and St Jean (1961, p. 68) considered that they possessed '. . . no internal characteristics of typical *Dermatostroma*' and indeed posed the question '. . . is *Dermatostroma* a stromatoporoid?' (ibid., p. 8). Nestor (1981, p. 23) suggested that these three species be transferred to the Protaraeida because of their pinnate fibrous microstructure, rather than a fibro-lamellar structure as in typical *Dermatostroma* and its close relative *Lophiostroma* Nicholson, 1891. Their heliolitid coral affinity is now confirmed by recognition of corallites in Anticosti Island specimens of two species. Previously described specimens of the three species of *Dermatostroma* (above) lack vesicular skeletal plates.

Except for *C. astomata* Flower the few species ascribed to *Coccoseris* in the literature bear less resemblance to the Anticosti Island species. Although internal skeletal details in some previous species are somewhat obscured by diagenetic effects, their corallites tend to be more distinct, both as slightly depressed calices externally and as inclined septal trabeculae in longitudinal section.

Status of Ellisites glyptum (*Parks*)

The name *corrugata* (*um*) was used by Foerste (July 1910, p. 86) for Richmondian specimens assigned to *Labechia*(?) from the '. . . Whitewater bed, along Dutch Creek, near Wilmington, Ohio . . .'. One large specimen from the same locality was distinguished as *L.* (?) *corrugataglypta* because of its irregular, vermiform surface ridges, and was subsequently designated a new species, *D. glyptum* Foerste (1916, p. 298). Parks (October 1910) used material from the same Ohio locality (specimens presented to the University of Toronto by A. J. Foerste) to establish *his* new genus and species *D. glyptum* and *D. corrugatum*, both of which had distinctive vermiculate surface ridges.

EXPLANATION OF PLATE 34

Fig. 1. *Ellisites astomata* (Flower). Hypotype, GSC 41177, Akpatok Island, unnamed Upper Ordovician limestones; tangential section showing regularly spaced clusters of smaller trabeculae representing corallite centres (compare text-fig. 3B), × 10.

Figs. 2–7. *E. glyptum* (Parks). 2, 3, hypotype, GSC 77915, GSC loc. 81821, Angling River, north-eastern Manitoba, Chasm Creek Formation; tangential section (2) showing prismatic trabeculae with fibrous microstructure, × 10; and exterior surface (3) showing one of several radial markings which superficially resemble astrorhizal systems, but which are consistent in size and configuration with outlines of inclined septal trabeculae within a corallite (compare with text-fig. 4), × 7·5. 4, 6, hypotype, ROM 17071 (817 H.R.) (holotype of *Dermatostroma corrugatum* Parks), Dutch Creek near Wilmington, Ohio, Whitewater Formation; tangential (4) and longitudinal (6) sections showing prismatic trabecular structure (note that the two growth laminae on fig. 6 grew in opposite directions), × 10. 5, holotype, ROM 17070 (816 H.R.), Dutch Creek near Wilmington, Ohio, Whitewater Formation; tangential section showing fibrous microstructure in several trabeculae, × 10. 7, topotype, IU302-15, Dutch Creek near Wilmington, Ohio, Whitewater Formation; longitudinal section showing fibrous microstructure in trabeculae of two thin growth laminae, × 10.

Figs. 8 and 9. *Coccoseris*? *escanabaense* (Galloway and Ehlers). Holotype and only known specimen, UM 39449 and thin sections IU308-98 and 308-99, Escanaba River, Delta County, Michigan, Middle Ordovician; tangential (8) and longitudinal (9) sections, × 10.

PLATE 34
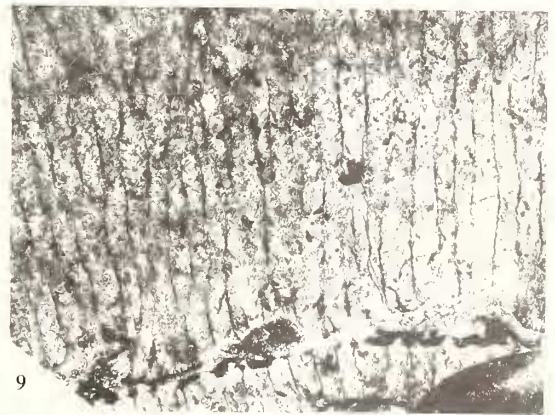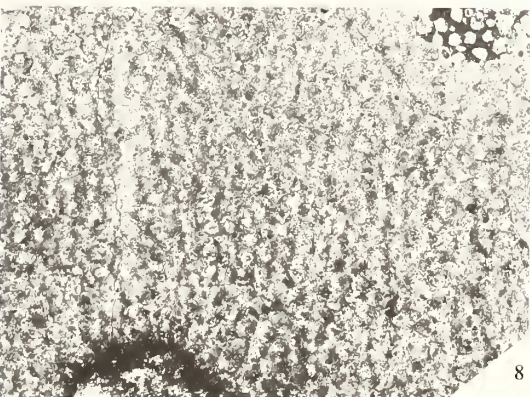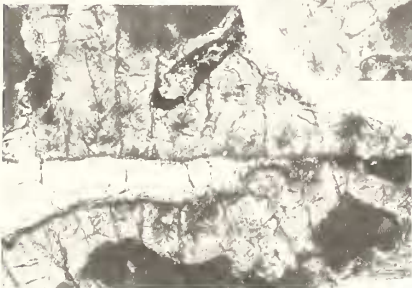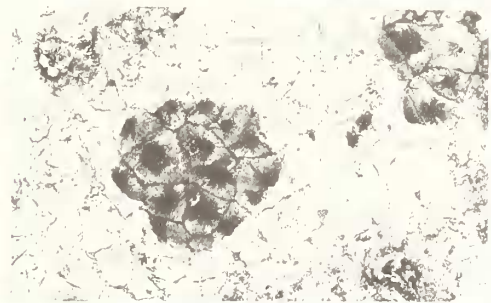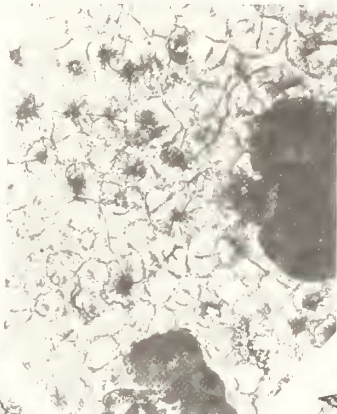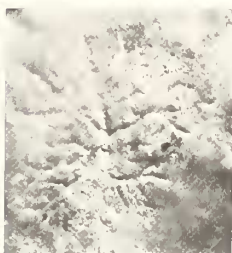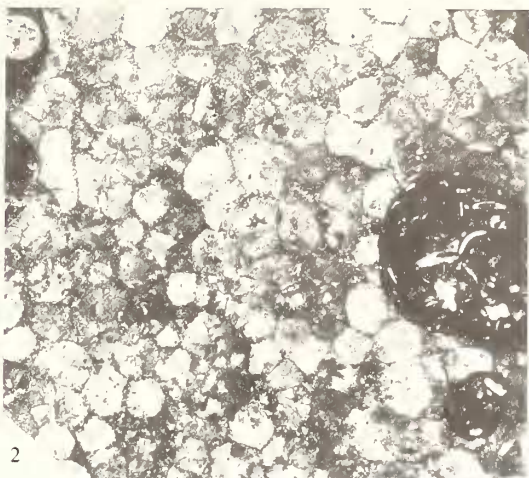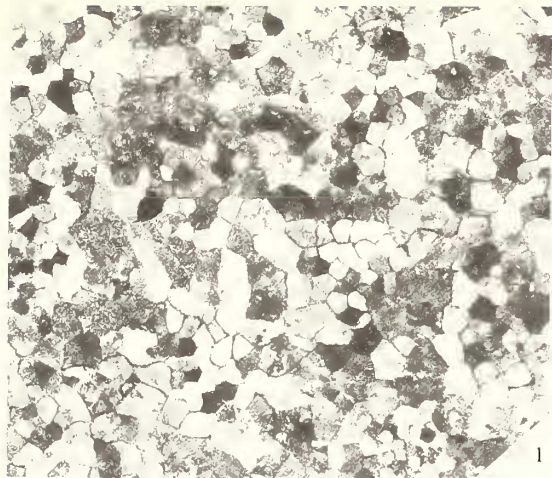
DIXON, BOLTON and COPPER, *Ellisites* and *Coccoseris*?

His holotypes in the Royal Ontario Museum differ from those illustrated by Foerste (1910, pl. 1, fig. 11; 1916, pl. 1, fig. 2). Both of Parks's species subsequently were assigned to *D.? glyptum* (Foerste) by Galloway and St Jean (1961, p. 72).

Our re-examination of these species and their nomenclatural problem made use of the following type specimens (Foerste's types not being located):

Type 816 H.R., University of Toronto Paleontology Collections (designated holotype, ROM 17070, of *D. glyptum* Parks 1910, p. 34).

Type 817 H.R., University of Toronto Paleontology Collections (designated holotype, ROM 17071, of *D. corrugatum* Parks 1910, p. 35).

Type 7665, slide 01-21, University of Michigan, Museum of Paleontology (designated topotype of *D.? glyptum* (Foerste, 1910) by Galloway and St Jean 1961, p. 73, pl. 10, fig. 2).

Slide 302-15, Indiana University Paleontology Collections (designated topotype of *D.? glyptum* (Foerste, 1910) by Galloway and St Jean 1961, p. 73, pl. 10, fig. 4*a, b*).

Slide 309-39, Indiana University Paleontology Collections (topotype of *D.? corrugatum* (Foerste, 1910) from collection of Galloway and St Jean). The topotype illustrated by Galloway and St Jean (1961) is designated slide 308-98 (apparently in error) on their p. 72, pl. 10, fig. 3*a, b*. The same number is quoted for a slide of the holotype of *D.? escanabaense* (ibid., p. 74) and the thin section of *D.? escanabaense* also bears number 308-98 (apparently correctly).

Type 39449, slides 01-23 and 01-24, University of Michigan, Museum of Paleontology; slides 308-98, 308-99, and a fragment, Indiana University Paleontology Collections (designated holotype and only known specimen of *D.? escanabaense* Galloway and Ehlers, *in* Galloway and St Jean 1961, pp. 73–74, pl. 11, fig. 1*a, b*; pl. 13, fig. 3).

We consider Foerste's descriptions and illustrations (1910, pp. 86–87, pl. 1, fig. 11; 1916, pp. 298–299, pl. 1, fig. 2) of the exteriors of two specimens to be inadequate to establish species characteristics. As the repository of his illustrated specimens is not known, we recommend that Foerste's trivial name *corrugata* (or *corrugataglypta*) be suppressed in favour of Parks's first designated name *glyptum*, for which an original description, illustrations, and usable holotype and topotype material are available.

According to our present understanding of intraspecific variability in *Ellisites*, holotype 816 H.R. (Pl. 34, fig. 5), holotype 817 H.R. (Pl. 34, figs. 4 and 6), topotype 7665 and slide IU 302-15 (Pl. 34, fig. 7) belong to the same species, as suggested earlier by Galloway and St Jean (1961, p. 72), and should be referred to *E. glyptum* (Parks), as explained above. In addition, slide IU 309-39, although described by Galloway and St Jean (1961, pp. 71–72) as *D.? corrugatum* (Foerste), was considered by them to be probably the same species as *D.? glyptum* (Foerste), the latter differing only in having vermiform surface ridges. We concur and regard this specimen as *E. glyptum* (Parks). The surface ridges noted appear to be merely growth interference at the edges of several encrusting sheets. Vesicular skeletal plates do not appear in these Ohio specimens probably because of the very thin encrusting character of the coenosteum. Topotype 7665 has recognizable calices on its upper surface.

Among specimens assigned in published literature to *C. astomata* Flower, most conform to the group of Anticosti Island specimens herein designated *E. astomata* (Flower), as summarized previously. Three others, however, are distinctly different, and their re-examination and comparison with Parks's types suggest that they belong to *E. glyptum* (Parks). Along with the previously cited specimens of *E. astomata* from the Edenian Bad Cache Rapids Formation of Melville Peninsula (Bolton 1977), is a third (GSC 42919: ibid., pl. 3, figs. 1 and 4) with distinctly larger trabeculae (0·75–0·9 mm diameter) and rare basal vesicles. Another specimen (GSC 77916), from the Edenian–Maysvillian Thumb Mountain Formation of the Hunting River area, Somerset Island (Dixon 1975—GSC loc. 89518), has trabeculae 0·56–0·84 mm in diameter. Along with the previously cited specimen of *E. astomata* from the Richmondian Chasm Creek Formation, Churchill River Group, of the Nelson–Angling rivers area, north-eastern Manitoba (Cumming 1975, p. 38; GSC loc. 81821), is another colony (GSC 77915; Pl. 34, fig. 2) with rare vesicles at various levels and larger trabeculae ranging in diameter from 0·38 to 0·8 mm. One surface of this 22·0 cm wide and 3·5 cm

thick colony displays minute radial markings (Pl. 34, fig. 3) of a size, spacing, and arrangement corresponding to outlines of septal trabeculae. These three specimens with larger trabeculae compare most closely with *E. glyptum* (Parks).

The holotype of *D.? escanabaense* is a coccoserid coral and is considered at present not to belong to *Ellisites*. The skeleton has solely vertical trabeculae with diameters (0·3–0·4 mm) and arrangement of fibres similar to those of *E. labechioides*, but in contrast, the trabeculae are wholly contiguous and the colony lacks evidence of vesicular skeletal plates (Pl. 34, figs. 8 and 9). The specimen is tentatively referred to *Coccoseris* and appears to be closest to forms ascribed to *P.* (= *Coccoseris*) *ungerni* by Sokolov and Tesakov (1984).

Evolution

Present collecting suggests that species of *Ellisites* have distinctive stratigraphic ranges. From known North American occurrences, *E. astomata* first appeared in the Edenian–Maysvillian and ranged up into the Richmondian. It occurs on Anticosti Island in the uppermost Vaureal Formation (Richmondian) along with the first *E. labechioides*. *E. labechioides* alone occurs in the lower–middle Ellis Bay Formation (Gamachian), where it has been found as high as beds 15 m beneath the Ordovician–Silurian boundary.

Ellisites may have evolved from a *Coccoseris*/*Protaraea* ancestor in the mid-Ordovician by beginning to incorporate vesicular plates in the buildup of its trabecular skeleton. The order of stratigraphic occurrence of Anticosti Island species of *Ellisites* suggests further that forms such as *E. labechioides* with predominantly vesicular skeletons are more likely to have evolved from earlier species such as *E. astomata* (or *E. glyptum*) with predominantly trabecular skeletons. The vesicular character in this group therefore appears to be a later rather than an earlier development in the evolution of the Coccoseridicae. The hypotype of *E. labechioides* (GSC 77917) from the Stony Mountain Formation of southern Manitoba, although differing somewhat from Anticosti material, conforms to this interpreted sequence in being a predominantly vesicular *Ellisites* at the younger end of the stratigraphic range of the genus in interior North America.

STROMATOPOROID RESEMBLANCES

Vesicular plates are a common space-filling device employed by various organisms in building skeletons from a basal surface. Rudist bivalves, richthofeniid brachiopods, cryptostome bryozoans, cystimorph rugose corals, proporid heliolitid corals, and labechiid stromatoporoids have all included these elements in calcareous skeletons. Only in the skeletons of some stromatoporoids and some heliolitid corals are such vesicular plates combined with vertical, rod-like trabeculae. This combination in the Ellisitidae has implications not only for the relationship of this group to the Proporicae but also for the discrimination of some of these corals from the conspicuously cystose labechiid stromatoporoids. *Cystostroma* Galloway and St Jean *in* Galloway, 1957 is part of a group including *Rosenella* Nicholson, 1886, *Aulacera* Plummer, 1843, *Labechia* Milne-Edwards and Haime, 1851, and others (*see* Galloway 1957, p. 420) in which a fundamentally cystose skeleton contains pillars developed to different degrees, from short denticles to long continuous rods to absent. Larger, wholly vesicular zones of the coenosteum of *E. labechioides* sp. nov. (Pl. 30, fig. 3; Pl. 31, fig. 2; Pl. 32, fig. 2) strikingly resemble some illustrations of *Cystostroma* in the literature (e.g. the upper Ordovician *C. cliefdenense* Webby, 1969, pl. 177, figs. 2 and 5; the middle–upper Ordovician *C. concinnum* Ivanov *in* Bogoyavlenskaya, 1973, pl. 3, fig. 1, with small sporadic villi or slender tubule-like pillars: Webby 1979*a*, p. 87).

The remarkable likeness of some of these corals to labechiids and the difficulty of distinguishing them is also illustrated by the specimens of *E. labechioides* referred by Bolton (1981, p. 42, pl. 1, fig. 4; pl. 2, figs. 1 and 2) to *Labechia* n. sp. aff. *L. mirabilis–L. banksi* group. Coenostea from the late Ordovician of Kolyma Basin, north-eastern USSR, consist of intergrowths of what have been defined as *L. mirabilis* Yavorsky and *C. rarum* Yavorsky (1961, pl. 19, figs. 2–6; pl. 20, figs. 1 and 2) that in many aspects appear similar to *Ellisites*, but the impersistent pillars are non-tubercular.

L. banksi Webby, 1979 similarly exhibits *Cystostroma*-like bands within normally cystose—denticulate—discretely pillared coenostea (Webby 1979*b*, p. 244).

Labechiids and other stromatoporoids, however, possess characteristic astrorhizal systems that cannot be explained in terms of a corallite structure. Astrorhizae have not been distinguished in any of the numerous well-preserved specimens of *Ellisites*. Minute radial grooves on the exterior of one of the specimens referred to *E. glyptum* (Pl. 34, fig. 3) bear a superficial resemblance to astrorhizae, but their size and configuration are consistent with them being the outlines of inclined septal trabeculae (their margins possibly emphasized by ground water solution). A comparable pattern of very similar size and character is shown by inclined septal trabeculae in a tangential section of a coccoserid from New South Wales (text-fig. 4).

Labechia developed long pillars in a cystose skeleton. The pillars are composed of '. . . loosely aggregated granular material . . .' (Galloway and St Jean 1961, p. 7), different from the pinnate fibrous microstructure of *Ellisites*, although diagenesis can reduce the latter to a dark granular texture not readily distinguishable from pillars in labechiids. *Labechia* shows some tendency for pillars to fuse along lateral surfaces (Bogoyavlenskaya 1971, p. 32) but far short of the extent shown by *Elllisites*. In most labechiids the initiation of pillars is staggered, although some (e.g. the Wenlock *L. communis* Yavorsky, 1963, pl. 9, fig. 3) show short pillars tending to begin at common levels. In all astogenetic stages of most genera (some species of *Aulacera* being exceptions), pillars appear to be the same in length, width, and number (Galloway 1957, p. 371). In contrast, *Ellisites* shows marked astogenetic change: most trabeculae begin at corresponding levels, and constitute sharply defined growth zones that are generally more frequent with maturity (e.g. Pl. 30, figs. 1 and 4; Pl. 31, fig. 2). Finally, some labechiids show differentiation of cysts into columns (e.g. by size in *Cystostroma*: see Bogoyavlenskaya 1973, p. 19). An analogous feature in *Ellisites* is the differentiation, in sectors of vesicular plates, of what are interpreted as columns of incomplete tabulae (in corallites) with intervening dissepiments (in coenenchyme).

In summary, the skeletons of *Ellisites* and labechiid stromatoporoids are very similar in combining vertical rod-like trabeculae and vesicular plates and in the character and disposition of these skeletal structures. In some well-preserved specimens of *Ellisites*, the presence of corallite calices, the internal arrangement of trabeculae suggestive of corallites separated by coenenchyme, and the absence of astrorhizal systems are characteristics of heliolitid corals rather than stromatoporoids.

CONCLUSIONS

1. *Dermatostroma*? *escanabaense* Galloway and Ehlers, *D. corrugatum* Parks, and *D. glyptum* Parks are interpreted as heliolitid corals rather than stromatoporoids, and are therefore excluded from *Dermatostroma* Parks.

2. *D. glyptum* and *D. corrugatum* are considered to be synonymous and are removed to a new genus, *Ellisites*, as *E. glyptum*, through comparison with material designated *E. labechioides* sp. nov. and *E. astomata* (Flower) from Anticosti Island.

3. *Ellisites* gen. nov. is placed in the Ellisitidae fam. nov., in the superfamily Coccoseridicae, and is interpreted as a phylogenetic link between this group and the Proporicae.

4. Earlier species such as *E. glyptum* and *E. astomata* (both Edenian to Richmondian) have predominantly trabecular skeletons with minor vesicular plates; the younger *E. labechioides* (Richmondian–Gamachian) has a strongly vesicular skeletal construction that deceptively mimics the characteristic cystose structure of labechiid stromatoporoids.

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APPENDIX

ANTICOSTI ISLAND LOCALITIES

Studied material was collected by T. E. Bolton—'BF' collections (numbers in parentheses) at localities 2, 3, 4, and 16; by O. A. Dixon—'J', 'M', and 'Q' collections at localities 1, 5, and 16; by R. Sanschagrin—locality 3c; and by P. Copper—'A' collections at localities 3c and 6 to 15.

1. Main highway, 40 km from Port Menier, at Ste Marie River. NTS Lac Faure 12E/13W, 3795 : 1890. Upper Vaureal Formation (M2-74). *Ellisites astomata.*

2. GSC loc. 36269. Jupiter River road (1958), 0·8 km south of main highway. NTS Anse de la Sauvagesse 12E/14, 6475 : 1245. Upper Vaureal Formation (BF82A). *E. astomata.*

3a. GSC loc. 36146. Main highway, 77·6 km from Port Menier. NTS Anse de la Sauvagesse 12E/14, 7025 : 1290. Upper Vaureal Formation (BF18). *E. astomata, E. labechioides.*

3b. GSC loc. 66774. Main highway, 1·6 km east of Jupiter River road (1964). NTS Anse de la Sauvagesse 12E/14, 7110 : 1210. Upper Vaureal Formation (BF188). *E. labechioides.*

3c. GSC loc. 76087. Main highway, 1·1 km east of Beaver Cove road. NTS Anse de la Sauvagesse 12E/14, 7388 : 1080. Upper Vaureal Formation (BF229D; A14). *E. astomata, E. labechioides.*

4. GSC loc. 76091. Loon Lake–Bear Lake road, just south of junction with main highway. NTS Lac Wickenden 12E/11, 7545 : 1020. Upper Vaureal Formation (BF229B). *E. labechioides.*

5. McDonald Fire Tower–Jupiter River road, 1·1 km south of main highway. NTS Lac Wickenden 12E/11, 8430–8445 : 0650–0690. Upper Vaureal Formation (Q10-74). *E. astomata*, *E. labechioides*.

6. Coastal cliff, waterfall, and tidal flat exposures in Mill Bay, 1·2 km east of Schmitt Creek. NTS Broom Bay 12E/8, 6780 : 7052(A202), 6620–6750 : 6960–7300(A365a). Upper Vaureal Formation, loose collection from cliffs (A202) and approximately 7–8 m below top (A365a). *E. astomata*.

7. Coastal exposures in Mill Bay, 1 km west of Schmitt Creek. NTS Broom Bay 12E/8, 6470–6580 : 6960–7020. Upper Vaureal Formaton, 3·5 m below top (A364/1—Copper) or basal Ellis Bay Formation (Bolton). *E. astomata*.

8. Tidal flat exposures at base of Prinsta Point cliff, 2 km north of Prinsta River. NTS Cap de la Table 12F/5, 7453 : 6811. Upper Vaureal Formation, uppermost 2 m (A133—Copper) or basal Ellis Bay Formation (Bolton). *E. astomata*.

9. Prinsta Point, loose blocks from cliff about 8·5 m above tidal flat. NTS Cap de la Table 12F/5, 7443 : 6775. Ellis Bay Formation, at least 19·5 m above base (A212). *E. labechioides*.

10. Shoreline and tidal flat exposures at base of waterfall, Prinsta Bay, about 2 km east of Prinsta River mouth. NTS Cap de la Table 12F/5, 7615 : 6618. Ellis Bay Formation, 20–21 m below Ellis Bay/Becscie formational boundary of Cocks and Copper (1981) (A138; A213). *E. labechioides*.

11. Coastal cliff and tidal flat exposures from west of Lousy Cove creek toward Table Head. NTS Cap de la Table 12F/5, 8085–8087 : 6488–6495. Ellis Bay Formation, approximately 25 m below Ellis Bay/Becscie formational boundary of Cocks and Copper (1981) (A219). *E. labechioides*.

12. Coastal cliffs about 1 km south of Table Head Lighthouse. NTS Cap de la Table 12F/5, 8052 : 6596. Same horizon as locality 11 (A220). *E. labechioides*.

13. Tidal flat exposure, north side of mouth of Table Head Creek. NTS Cap de la Table 12F/5, 8092 : 6478. Same horizon as locality 11 (A315; A357/2). *E. labechioides*.

14. Low cliff exposures, south side of mouth of Table Head Creek. NTS Cap de la Table 12F/5, 8096 : 6468. Ellis Bay Formation, 21 m below Ellis Bay/Becscie formational boundary of Cocks and Copper (1981) (A218). *E. labechioides*.

15. Low cliff exposures, east side of Prinsta River mouth. NTS Cap de la Table 12F/5, 7448 : 6645. Ellis Bay Formation, 15 m below Ellis Bay/Becscie formational boundary of Cocks and Copper (1981) (A135). *E. labechioides*.

16. GSC locs. 84385 and 92401. Vaureal River, 3·8 km south-south-west from Vaureal Falls. NTS Carleton Point 12E/10, 2045 : 8630. Ellis Bay Formation, member 4 (BF403; J2-74). *E. labechioides*.